

THE AFFINITIES OF TYMPANOCRYPTIS MACULOSA MITCHELL (LACERTILIA-AGAMIDAE)

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Figs. 1-2

SYNOPSIS

Cleared and stained skeletal material is used to compare the osteology of 14 species of the genera *Amphibolurus* and *Tympanocryptis*, and thereby reassess the generic status of the dragon described as *Tympanocryptis maculosa* Mitchell (1948).

It is concluded that the closure of the tympanic membrane is a secondary feature and that species referred to the genus *Tympanocryptis* should be primarily distinguished by the reduction of one phalanx of the fifth digit of the pes. Despite its possession of a concealed tympanic membrane and other features most strongly developed in *Tympanocryptis*, *maculosa* agrees with *Amphibolurus* in possessing primitive phalangeal formulae and is now considered a specialized member of that genus.

INTRODUCTION

In naming and defining the genus *Tympanocryptis*, Peters (1863) emphasized the closure of the tympanic opening and the absence of femoral pores as generic characters, and the combination of these two features proved a practical means of isolating a small number of species for taxonomic purposes. The description of *T. tetraporophora* Lucas and Frost, a species possessing one femoral pore on each side was accepted because of its obvious close relationship to the orthotype, *T. lineata* Peters. However, the description of a species with a concealed tympanic membrane, but possessing 5-8 femoral pores on each side and an *Amphibolurus*-like general habit as *Tympanocryptis maculosa* Mitchell, the close superficial resemblance between several spinous scaled species of *Amphibolurus* and recently described species of *Tympanocryptis*, and the discovery of an agamid (identity as yet

uncertain) possessing partial concealment of the tympanic membrane have cast doubt on the value of the enclosed ear-opening as the indicator of a monophyletic assemblage.

The present study was undertaken in an effort to find alternate means of defining these genera and, in particular, of reconsidering the generic status of *maculosa* on the basis of comparative skeletal morphology.

METHODS AND MATERIAL EXAMINED

Skeletons were prepared by standard clearing and alizarin staining techniques permitting calcified parts of the anatomy to be clearly distinguished. Cartilaginous parts were not differentially stained.

Five skeletons of *T. maculosa* were prepared from specimens varying in snout-vent length from 28 mm to 65 mm and compared with the following specimens in the South Australian Museum reference collection.

Species with an exposed tympanum:

Amphibolurus adelaidensis (Gray)—Two adult specimens collected at Eyres Sand Patch, Western Australia.

Amphibolurus reticulatus inermis (De Vis)—One subadult specimen collected at Muloorina, South Australia.

Amphibolurus maculatus gularis Sternfeld—Two adult specimens collected at Wolf Creek, Western Australia.

Amphibolurus pictus Peters—Three specimens; one subadult collected at Mount Eyre; one adult from Tailen Bend and one adult from Western Gawler Ranges, South Australia.

Amphibolurus diemensis (Gray)—Two adult specimens collected at an unknown locality in Tasmania.

Amphibolurus darlingtoni Loveridge—One adult specimen collected at Ooldea, South Australia.

Amphibolurus cristatus (Gray)—One subadult specimen collected at Koonibba, South Australia.

Amphibolurus decresii (Dunn. and Bibr.)—Two specimens; one subadult and one adult collected at Mount Aroona, Flinders Ranges, South Australia.

Amphibolurus fionii Proctor—One adult specimen collected at Mount Wedge, Eyre Peninsula, South Australia.

Species with a concealed tympanum:

Tympanocryptis letroporophora Lucas and Frost—Two adult specimens collected near Leigh Creek, Flinders Ranges, South Australia.

Tympanocryptis intima Mitchell—Three adult specimens; two collected at Finmiss Springs and one at Etadunna, South Australia.

Tympanocryptis lineata lineata Peters—Two adult specimens; one collected near Port Lincoln, and the other near Adelaide, South Australia.

Tympanocryptis cephalus gigas Mitchell—One adult specimen collected in the Murchison District, Western Australia.

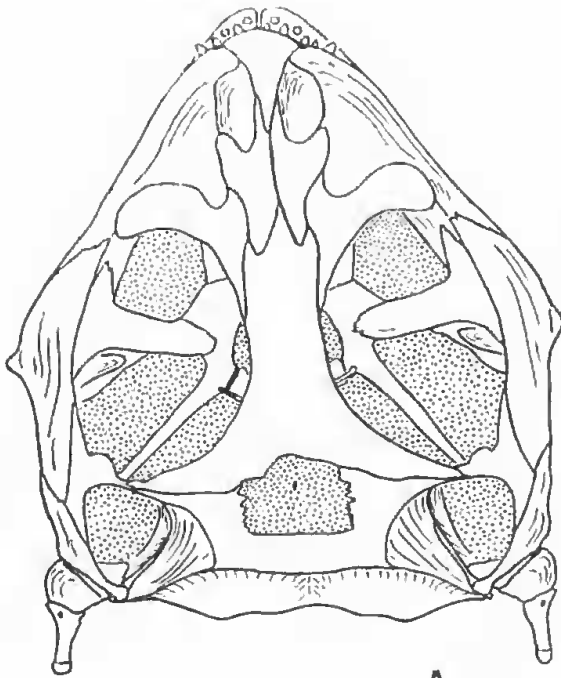
SKELETAL MORPHOLOGY

The following is a summary of the variation observed in a number of key features which were considered adequate to provide a guide to affinities.

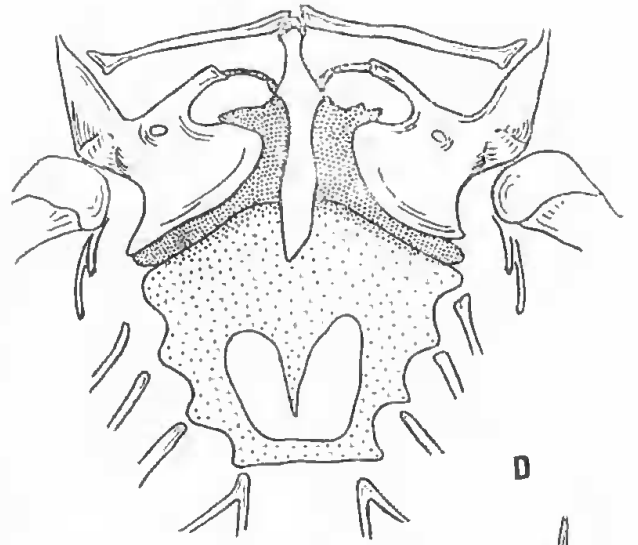
The general skeletal morphology is relatively uniform and the range of variation appears to be in part correlated with body form and related behaviour. While possessing the basic pattern of *Amphiholurus*, the skeleton of *T. maculosa* shows several of the specializations most strongly developed in *Tympanocryptis*. Its skeletal detail is figured in fig. 1 and used as the main point of reference.

The Skull: The cartilage bones roofing the skull are subject to little variation other than relative proportions. The extent of penetration of the paired nasals between the prefrontals and the penetration of the premaxilla between the nasals are subject to interspecific variation. The relative proportions of the premaxilla appears to be constant and diagnostic, varying at the extremes from long, slender and acute in *A. maculatus gularis* through long, parallel sided and rounded in *A. diemensis* to short, wide and obtuse in *A. reticulatus inermis*.

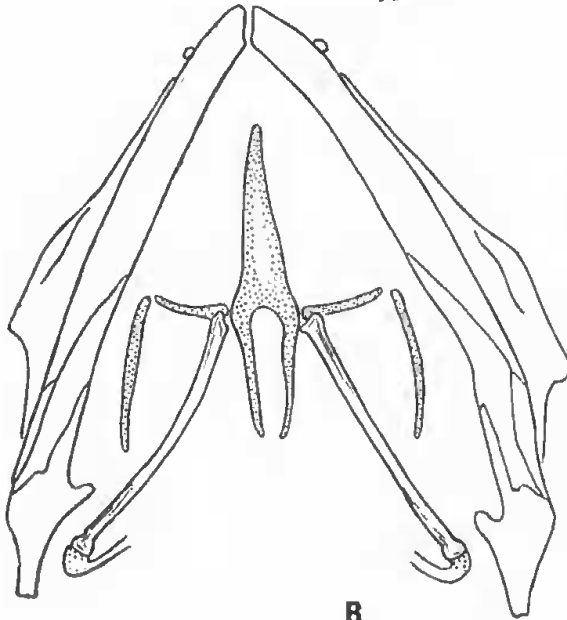
Beddard (1905) accepted the osteology of *A. barbatus* as typical of the genus and used it as part of the foundation for his comparison with *Chlamydosaurus*. Apart from the fact that lizard osteology is subject to greater interspecific variation than was suspected by Beddard, the examination of several dried skulls supports Beddard's



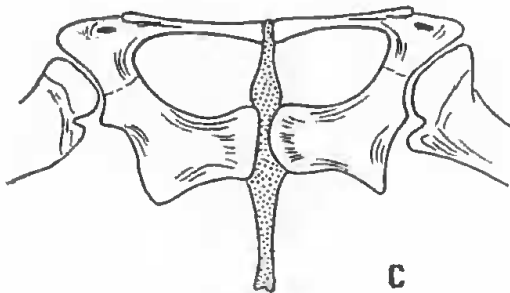
A



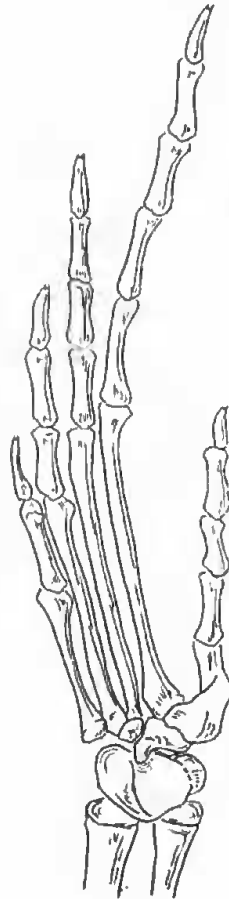
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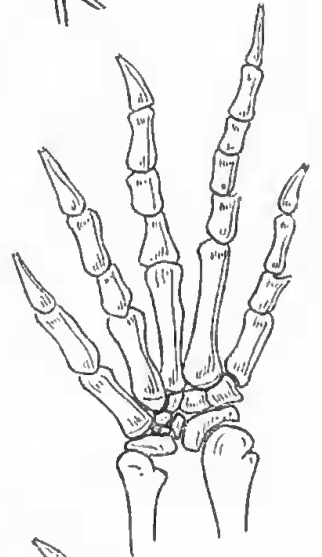
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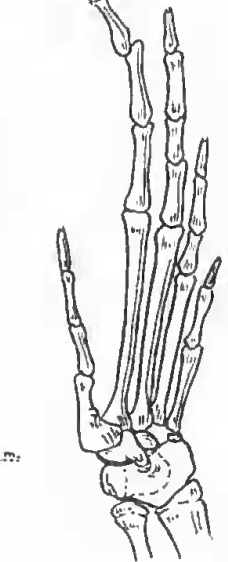
C



E



G



F

0 5 mm

comparisons, but reveals *barbatus* to be atypical of the genus as a whole in several respects. The palatines meet on the midline in adult *barbatus* and Beddard contrasted this with the condition in *Chlamydosaurus*. In all species examined in the present study the palatines were clearly separated on the midline. Also, the premaxillary bone usually fails to reach beyond the posterior margin of the external nares and frequently it only extends approximately two-thirds the way along the median border. Species with short, wide premaxillas, such as *A. reticulatus incermis*, possess small external nares to match.

The parietals are invariably fused posteriorly but display wide variation in the size and form of the parietal foramen, which is greatly enlarged and emarginate anteriorly in most species. In many species there is also retardation or failure of ossification in median parts of the posterior border of the frontal (see fig. 1). In fully adult specimens of several species examined, *T. lineata*, *A. pictus*, *A. decresii* and in one each of the two specimens of *A. diemensis* and *A. adelaidensis* the parietal foramen is a simple perforation at or immediately behind the centre of the fronto-parietal suture.

In the large and probably senile specimen of *A. pictus* from Tailem Bend, South Australia, the perforation is in a backward extension of the frontal which intrudes the transverse line of the normal fronto-parietal suture to fill the parietal foramen. In all other species examined this foramen is enlarged to varying extents, and a large part of the cranial cavity remains unprotected through to adulthood. The relative size and shape of the parietal opening appears constant for adult specimens and could be of diagnostic value if required. The ontogenetic sequence of *T. maculosa* clearly shows the latter stages in the ossification of the parietal and indicates that the enlarged foramen undergoes little change in relative size or shape during development in this species. This feature is most strongly developed in species inhabiting open stony or sandy desert.

Fig. 1. *Tympanocryptis maculosa* (adult male)

- A. Dorsal view of the skull oriented so that the frontal is at 90° to the angle of view.
- B. Ventral view showing the relationship between the lower jaws and the hyo-branchial apparatus.
- C. Pelvic girdle.
- D. Pectoral girdle.
- E. Pes of *Tympanocryptis maculosa*.
- F. Pes of *Tympanocryptis lineata* shown for comparison.
- G. Manus of *Tympanocryptis maculosa*.

The bones comprising the superior temporal arch vary considerably from one species to another. The jugal and post-orbital bones are in part compensatory in size and shape. *T. lineata*, *T. tetraparophora*, *T. intima*, *T. cephalus gigas* and *A. diemensis* possess enlarged jugals extending well upward into the temporal arch; *A. adelaidensis* possesses an enlarged jugal which is wide but not high. In *T. cephalus gigas* and *A. adelaidensis* the post-orbital bridge is conspicuously wide. In *A. maculatus gularis*, *A. cristatus*, *A. darlingtoni*, *A. reticulatus* and *T. maculosa* the jugal is comparatively slender and does not extend as far up the arch, the post-orbital frequently extending downward along the margin of the orbital vacuity. The post-frontals are absent.

The form of the remnant of the supratemporal in relation to the superior articulation of the quadrate is of interest. The supratemporal is rather superficially attached to the parietal process in *maculosa*, but in the majority of species it is a flattened splinter embedded in the lower lateral edge of the process. Its distal end passes under the squamosal where it thickens to articulate against the quadrate. In *A. flouii* and *A. decresii* the quadrate articulates well forward on the squamosal and the enlargement of the supratemporal under the squamosal is quite considerable.

The dentition is heterodont, the posterior 12 or 13 teeth in both upper and lower jaws being acrodont and strongly compressed and the anterior teeth subthecondont and conical. In *A. cristatus*, *A. diemensis* and to a lesser extent in *A. maculatus gularis* the posterior acrodont teeth are enlarged and tend tricuspid. Each central cusp is sharply pointed and the lateral cusps are flat or only slightly raised. The upper jaw closely overlies the lower jaw, the central cusps of the six enlarged posterior upper teeth interlocking into grooves in the outer face of the dentary. In *T. cephalus gigas* and *T. intima* the enlarged teeth in the upper jaw are inclined slightly so that the teeth themselves interlock. In both of these species the size of these teeth decreases rapidly towards the front and anteriorly are kept permanently separated by the interlocking of the enlarged incisors.

The first and second maxillary, first and second mandibular and the two or three premaxillary teeth are conical in all species except *A. cristatus* which appears to lack conical mandibular teeth. These teeth are firmly attached to the bone at the base, but are separated by porous bony septa. In all species referred to *Tympanocryptis*, including *maculosa*, they are considerably enlarged and slightly

recurved. An enlarged mandibular tooth fits into a notch in the upper jaw between the maxilla and the premaxilla on each side, and an enlarged maxillary tooth functions as a canine and overlies the dentary on each side. The lower jaw is slightly longer than the upper jaw to allow these teeth to interlock in this manner (see fig. 1).

Hyobranchial Structure: The hyoid displays little variation from that figured for *maculosa* (fig. 1). The first branchial arch is strongly developed in all species examined, the bony ceratobranchial articulating on the body of the hyoid.

Because non-calcified cartilaginous structures were not adequately differentiated in the material studied it was not possible to trace the epibranchial I elements, but in several species, *T. maculosa* (see fig. 1), *T. lineata*, and *T. tetraporophora* the ceratobranchial-epibranchial connection is very strong and the epibranchial can be seen turning abruptly away in a manner which suggests that it joins the cranial wall near the auditory structures. The ceratobranchial is also strongly developed in several species of *Amphibolurus* examined, but the epibranchial connection is usually weaker and situated further behind the quadrate.

Assuming the closure of the ear membrane reflects the need for substantial modification of the auditory mechanism, a detailed study of cartilaginous parts of the branchial arch and of the structure of the auditory capsule may reveal some significant parallels.

Pectoral Girdle: The detail of this girdle is composed of both stable and unstable characters. All species possess simple rod-like clavicles with no median fenestrae, have the scapula and coracoid fused in the adult, have a supra-coracoidal foramen, a lateral coracoidal fenestra formed by the extension of the calcified cartilage of the epicoracoid to join the anterior corner of the coracoid and a very distinct and heavily reinforced articulating glenoid for the forelimb.

The number of sternal ribs is three on each side in the majority of species with one rib attached to each xiphisternal horn, but some variation was noted. *A. maculatus gularis* possesses four sternal and no xiphisternal ribs; *T. tetraporophora* and *A. darlingtoni* also possess four sternal ribs, but the lower pair in each case are attached at the base of the xiphisternum. This also applies to one of the two specimens of *A. diemensis*. Single specimens of *A. pictus*, *A. adelaidensis* and *T. intima* possess three sternal but no xiphisternal ribs. The ribs are attached to the 9th, 10th, 11th and 12th vertebrae.

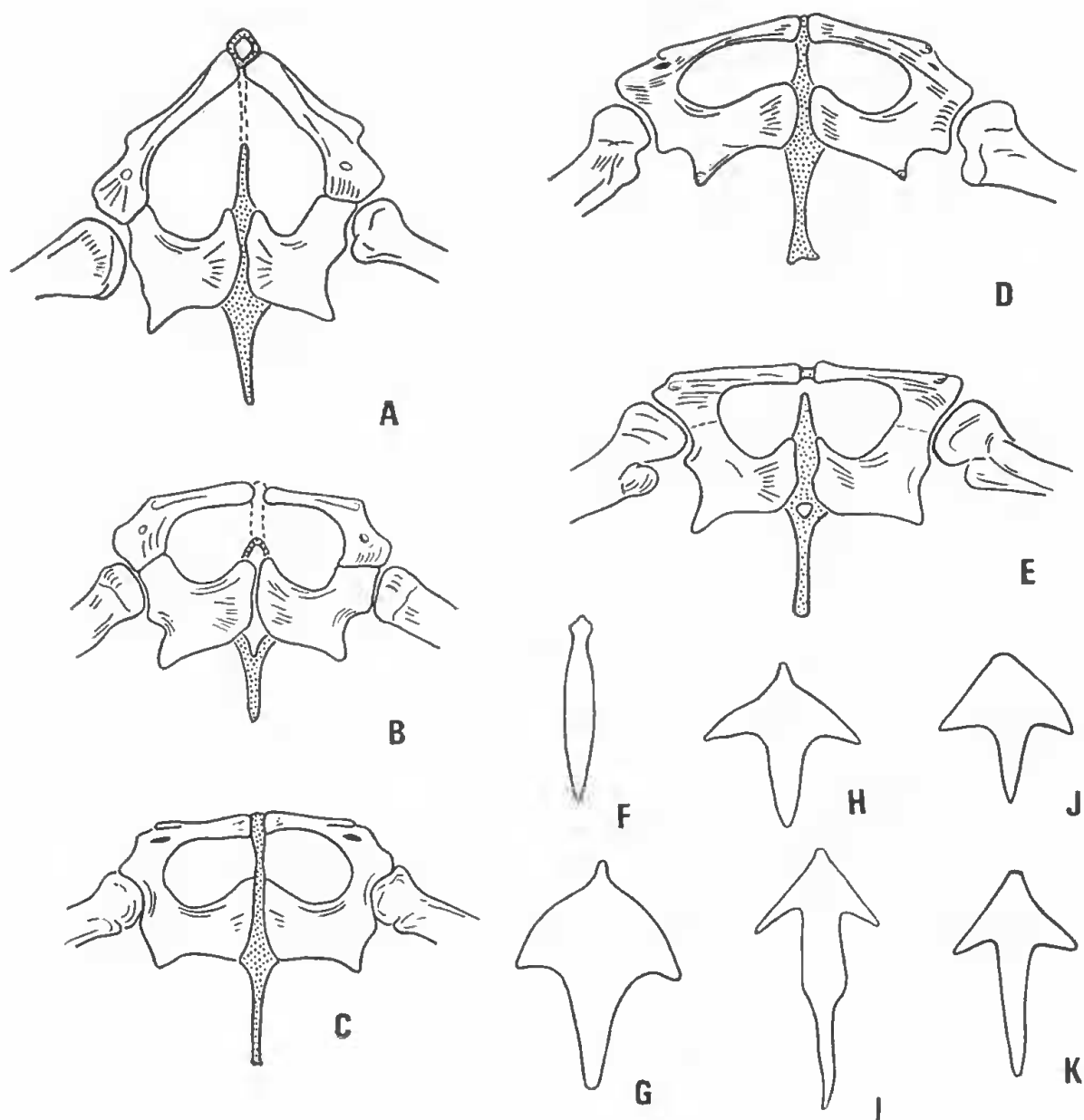


Fig. 2.

Pelvic Girdles of:—

- A. *Amphibolurus maculatus gularis*.
- B. *Amphibolurus pictus*.
- C. *Amphibolurus adelaidensis*.
- D. *Tympanocryptis lineata*.
- E. *Tympanocryptis intima*.

Interclavicles of:—

- F, G. *Amphibolurus pictus*.
- H. *Amphibolurus adelaidensis*.
- I. *Amphibolurus maculatus gularis*.
- J. *Tympanocryptis tetraporophora*.
- K. *Tympanocryptis lineata*.

The interclavicle is subject to wide variation, but the limited material available for study did not permit its interspecific stability to be adequately assessed. It varies from broad, short, arrow-shaped in *T. lineata* (fig. 2J), *T. tetraporophora* and *T. cephalus gigas* to broad, short, tending cruciform in *A. adalaidensis* (fig. 2H), *A. fionii* and *A. decresii* to long, arrow-shaped in *T. intima* (fig. 2K), *A. maculatus gularis* (fig. 2I), *A. reticulatus*, *A. darlingtoni* and *A. diemensis* to dagger-shaped in *T. maculosa* (fig. 1D) to simple blade-shaped in one specimen of *A. pictus* (fig. 2F) collected at Mount Eyre, South Australia. The interclavicle of *A. pictus* appears to be subject to wide individual variation. The interclavicle of the Western Gawler Range specimen is figured (fig. 2G) and that of the Tailem Bend specimen is long and broadly arrow-shaped (similar to fig. 2K). The interclavicle of *T. maculosa* is constant for the five specimens examined. *A. cristatus* has an unusual interclavicle. It is dagger-shaped with two oblique club-shaped lateral projections commencing two-thirds the way down the "handle".

Pelvic Girdle: Within the limitations of the material available for study the pelvic girdles appear constant and vary sufficiently to be of value as supporting data in species taxonomy.

The pubis and ischium are indistinguishably fused in adults of *A. adalaidensis*, *T. lineata* and *T. cephalus gigas* and retain a faint suture in young adults but are probably indistinguishably fused in senile specimens of *T. intima* and *T. maculosa*. Adults of *T. tetraporophora*, *A. decresii* and *A. fionii* possess firmly united bones but retain distinct sutures, while *A. maculatus gularis* (fig. 2A), *A. pictus* (fig. 2B), *A. darlingtoni* and in subadults of *A. cristatus* and *A. reticulatus inermis* these bones are clearly separate. The girdles of *A. cristatus* and *A. darlingtoni* are "open" structures similar to that figured for *A. maculatus gularis* (fig. 2A).

In the majority of species the ischio-pubic fenestra is divided by a strong cartilaginous structure involving both the hypo-ischium and the epipubis. In *T. lineata*, *T. tetraporophora*, *T. maculosa* and *A. adalaidensis* this median structure is heavily calcified throughout (see fig. 2), but in *A. maculatus gularis*, *A. reticulatus inermis*, *A. cristatus*, *A. fionii* and *A. decresii* calcification only occurs at the pubic and ischial ends. In *T. cephalus gigas*, *T. intima*, and *A. diemensis* the ischio-pubic fenestra is not completely divided.

The pubis is pierced by an obturator foramen, but because of the shape of the pubic bones this is partly or completely obscured in some species. When the girdle is viewed ventrally, the anterior process is transversely compressed and curves upward and outward in the form of a prepubic lip, on the lateral end of which is attached a ligament connected obliquely across to a point on the corresponding ischium. In species in which the process is strongly compressed and the lip well developed—*T. intima*, *T. lineata*, *T. tetraporophora*, *T. maculosa* and *A. adelaidensis* the obturator foramen is directed forward. In *T. intima* the foramen is directly below and completely concealed by the prepubic lip (see fig. 2). Of the species of *Tympanocryptis*, *cephalus gigas* is the only species examined which does not possess this feature. It possesses a very narrow girdle with the obturator foramen situated well below and across from the prepubic lip, being clearly visible when the girdle is viewed squarely from below.

Limb Structure: The structure of the forelimb was found to be constant, the primitive reptile formula of 2,3,4,5,3 being retained for the manus of all species examined.

Examination of hindlimb structure revealed the only clearly definable dichotomy evident from this study. All species of *Amphibolurus* examined possessed the primitive 2,3,4,5,4, formula for the pes while all species of *Tympanocryptis*, except *maculosa*, show a reduction of one phalanx in the fifth toe to a formula of 2,3,4,5,3. *T. maculosa* retains the primitive formula for both manus and pes.

There does not appear to be any significant variation in tarsal or carpal structure. The astragalus and calcaneum are fused in adults, but the suture is frequently distinct. These two bones are separate in juveniles of *T. maculosa*.

Vertebral Column: The number of presacral vertebrae (including the atlas) varies from 21 to 24 (see also Mitchell, 1948). The majority of species possess twenty-two, but the following exceptions were noted. *T. lineata* (21 and 23), *T. tetraporophora* (21 and 23), *A. adelaidensis* (21 and 23), *A. cristatus* (23) and *A. reticulatus inermis* (24).

The atlas has paired neurapophyses which are widely separated in most species. All presacral vertebrae except the atlas and three cervicals have ribs attached. There is much variation in the relative size and form of the neural spines, the spines being conspicuously

larger in long-limbed species possessing "open" type pelvic girdle structure (see fig. 2A) such as *A. maculatus gularis* and *A. cristatus*. This may be related to their ability to adopt a bipedal mode of locomotion.

DISCUSSION

Of the features examined, only the hindlimb structure shows a definable dichotomy which can be clearly correlated with taxonomic characters currently in use. The variation in all other features shows varying degrees of overlap between species in the two genera.

To further assist in determining the stability of the phalangeal structure, two unique specimens in the South Australian Museum collection were radiographed. The holotype of *T. uniformis* Mitchell, which is superficially unlike any other member of the genus, was photographed under X-rays and proved to be typical of the genus. It has a reduction of one phalanx in the fifth digit of the pes. A small dragon collected at the Silverband Falls, Grampians, Victoria and registered No. R3294 in the South Australian Museum collection shows close superficial similarity in size, scalation and colouration to *T. lineata* Peters, but differs in possessing a tympanic membrane which is only partially concealed and in having four or five femoral pores on each side. The whole membrane appears to be covered by a thin veneer of epidermal tissue, the central and upper parts of which are thickened, scaly and pigmented to match the surrounding epidermis. The radiograph of this specimen revealed no reduction in the number of phalanges of either manus or pes.

The support of *T. uniformis* leaves no doubt that the reduction of one phalanx in the pes in combination with the external features currently used to delimit *Tympanocryptis* will serve to maintain it as a useful taxonomic unit. Whether or not it is safe to assume a monophyletic origin for the species so grouped must remain a matter of opinion until more is known about the interspecific stability of osteological characters in this family.

Hypophalangy has been recorded as a species character in other families. Stephenson (1960) records variation in the formulae for both manus and pes in two species of the genus *Nephaurus* (Gekkonidae); Mitchell (in press) records the loss of one phalanx in the manus of a species of *Diptodactylus* (Gekkonidae); Mitchell (1955 and unpublished data)—progressive hypophalangy in both manus and pes is an important aspect of speciation in the Scincidae.

The discovery of a further species of *Amphibolurus* obviously not closely related to the progenitors of *maculosa*, which is developing a close resemblance to *Tympanocryptis* including a scaly covering for the ear membrane suggests that this feature is a recent and secondary development.

Within the range of variation recorded, *Tympanocryptis* species lie near one extreme and are subject to less interspecific variation. Features usually combined, such as the strong development of the bones in the superior temporal arch, the enlargement and interlocking of the conical anterior teeth, the short, wide, arrow-shaped interclavicle and the form of the pelvic girdle are characters developed independently in *Amphibolurus* species.

The species *maculosa* agrees with *Tympanocryptis* in dentition, pelvic girdle structure and concealment of the tympanum, but is typical of short-limbed species of *Amphibolurus* in all other respects. It is therefore proposed that *maculosa* be regarded as a specialized member of that genus. As such it would become *Amphibolurus maculosus* (Mitchell). The closeness of the specific names *maculosus* and *maculatus* is regrettable, but both appear to be admissible under the International Rules of Zoological Nomenclature.

ACKNOWLEDGMENT

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RESUME

Dans ce travail on traite et illustre l'anatomie de l'esquelllette de l'agamide *Tympanocryptis maculosa* Mitchell (1948). Comme resultat des comparaisons faites entre cette espèce et autres des genres *Tympanocryptis* et *Amphibolurus* on transfère *maculosa* au *Amphibolurus*.

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